VII. *An Instance of Mutation:* Coccus viridis, *Green, a Mutant from* Pulvinaria psidii, *Maskell.* By K. Kunhi Kannan, M.A., F.E.S.

[Read March 6th, 1918.]

Plates V—VIII.

Summary.

Coccus viridis, Green, has seven segments in the antennae. This was so in the Mysore specimens when the pest first appeared in the State in 1912. But specimens collected in 1913 and afterwards, though undoubtedly *C. viridis* in other respects, showed in the antennae a reduction to three segments by the coalescence of the terminal five into one. This indicated an instability in the species, which has now been placed beyond a doubt by the fact that there are in Java, besides the typical *C. viridis*, two distinct types, with very variable but usually eight antennal segments, highly unstable and with a host of intermediate forms. A new form from Uganda, described first as a subspecies, has been recently given specific rank by Newstead. *C. viridis* is therefore clearly unstable.

Pulvinaria psidii is also very variable in size, antennae, and anal plates, and some variations distinctly recall those of *C. viridis*. The chief distinguishing feature, of the secretion of meal for oviposition, may also be absent. *P. psidii* has, moreover, at least two subspecies. The gap between *P. psidii* and *C. viridis* being bridged over by the variations in both these, involving the same structures, and being in the same direction, *P. psidii* is the mutating species, *C. viridis* and its variants being derived directly or indirectly.

Similar relations between species in *Coccidae* have been noticed by others, and are best explained by the theory of Mutation applied as above. An exact parallel to the phenomenon, which occurred in *C. viridis*, has been noticed by Green in *Phenacoccus mangiferae*. The relations described by Quayle, of the University of California, between *Coccus citricola* and *C. hesperidum* are also similar to

those between *P. psidii* and *C. viridis,* and are similarly explained by the theory of regressive mutation.

The two insects dealt with in this paper belong to two closely allied genera in the order *Coccidae.* They are flat, oval scale or scab-like bugs, which are provided with hair-like tubes for feeding on plant sap. The adults show little trace of segmentation. They have three pairs of legs, a pair of segmented antennae, a pair of eyes, and two pairs of spiracles, which are situated a little distance from the margin, but are connected with it by shallow grooves called stigmatic clefts. At the place where the grooves touch the margin there are three stout spines, of which the central spine is twice the size of the other two. At short intervals along the entire margin, there are smaller spines which are dilated or toothed at the extremity. The anus is about a sixth of the distance from the margin, and is guarded by two triangular chitinous plates known as the anal plates, which lift up and open apart when there is a discharge. From the anus, in a line with the opening of the plates, there runs to the margin, a cleft dividing the posterior end into two lobes. The chitin of the dorsum has a definite pattern made up of what are called dermal cells, which are depressions or pits * of different shapes varying from irregularly oval to round. *Coccus viridis* is viviparous, the eggs developing inside the body and hatching usually at the time of discharge. *Pulvinaria psidii,* on the other hand, secretes a cottony waxy stuff to lay eggs in.

Coccus viridis, or green bug, is a serious pest of Coffee, which appeared in Ceylon so far back as 1882, and had no small share in the destruction of Coffee there. It has since appeared in the Pulneys, the Shevroys, the Nilgris, and finally in Mysore and Coorg. It feeds on a large number of plants, besides Coffee, viz. Tea, Guava, Citrus plants, Cinchona, several species of *Manihot, Gardenia, Ixora, Plumiera, Eugenia, Loranthus, Antidesma,* and several varieties of garden shrubs.

* The dermal cells cannot be correctly described as "depressions or pits." They are actual cells in the chitinous substance of the derm, each cell communicating with the surface by a minute pore. They have no connection with the superficial depressions (usually of a more or less polygonal form) that may be observed on the dorsum of the living insect.—E. E. G.

Pulvinaria psidii is known popularly as the "mealy bug"* for the reason already mentioned, that it secretes a large quantity of waxy substance which appears like cotton and forms a sort of cushion beneath the abdomen of the insect, lifting it up and bringing it at an angle to the surface of the leaf. The eggs are laid in this mass. Like green bug, it is quite at home on a variety of plants, viz. Coffee, Tea, Cinchona, Citrus plants, *Eugenia*, Guava, Myrtle, *Ficus*, Cardamom, *Duranta*, *Garcinia*, *Antidesma*, *Alpinia*, and numerous other plants.

Both these species have been studied in the Entomological Section of the Department of Agriculture in Mysore, ever since *Coccus viridis* appeared as a pest in the State in 1912, and this paper attempts to give some of the results of the investigation and their explanation.

When the pest first appeared, a number of planters sent in specimens for identification. All these were determined as *Coccus viridis*, as they answered in all respects to the description of the species given by Green in his book "The Coccidae of Ceylon." About a year afterwards, when specimens happened to be microscopically examined again, a remarkable change had appeared. The antennae, which are seven-segmented in the species, showed a reduction to three by the coalescence of the five apical segments into one. Several hundreds of specimens from all parts of the State were then examined, but none with seven-segmented antennae were found. From one estate, however, from which specimens were obtained immediately on the outbreak of the pest there in 1913, a few bugs were obtained which showed four or five segments in the antennae (Pl. VII, fig. 4, drawing i). Specimens from the Pulneys, Shevroys, the Nilgiris, and Coorg have also been examined, and all show a reduction to three segments, though in some there are traces of additional segmentation. There is little doubt, therefore, that in South India the three-segmented condition of the antennae is practically universal, though there is one important exception to which reference will be made later.

The reduction may make it appear probable that the bugs originally identified by Dr. Coleman and myself were not the same as the bug described by Green. Since,

* *Pulvinaria psidii* may be locally known as "mealy bug" in Southern India; but that term is more usually applied to members of the genus *Pseudococcus* and its allies.—E. E. G.

however, a seven-segmented antenna is one of the specific characters relied on by Green, a reduction had it occurred then would not have passed unnoticed. Moreover, a photograph of one of these earlier specimens fortunately shows seven distinct segments (Pl. V, fig. 1). There is little doubt, therefore, that the present form is derived from the typical *Coccus viridis*.

The reduction is not a character acquired by the adult, but appears in nymphs just hatched. This is remarkable, since Green mentions as a characteristic of not only the genus *Lecanium* (*Coccus*) but of all the genera in the family that the nymphs have six-segmented antennae, and as regards *Lecanium* (*Coccus*), he says, "the facts seem to indicate a primitive six-jointed antenna." Maskell, another authority, considers that six is the normal number of segments in all Coccids. The number six in the young persists in the adult, or is increased by a few more, but is seldom reduced.

Save for the inherited degeneration in the antennae, the Mysore form is identical with the bug from Ceylon in all microscopical details. The Ceylon specimens, obtained recently, are smaller in size. It is also probable that their reproductive powers are limited. Green says the bug produces only about 20,* whereas in Mysore the number has reached over 500. But these are minor details which do not affect the structural identity of the two forms except as regards the antennae.

Closely allied to the Ceylon form in sex, colour, and antennae, specimens were obtained from one citrus plant in Bangalore in May 1916. Periodical examination of specimens from this plant have been made since, and so far the reduction to three has not yet appeared, though there seems to be a tendency for the third and fourth, and fifth and sixth to coalesce. These specimens are therefore the typical *Coccus viridis* of Green. Save for this one instance a three-segmented condition of the antennae appears to be universal in the South Indian form.

It is remarkable that this seven-segmented condition should be found to persist in bugs collected in 1916 in

* I do not know where the author obtains his authority for this statement. I can find no such remark in my description of the species ("Coec. Ceylon," iii, p. 200). On the contrary, I have distinctly stated (*loc. cit.*) that "a constant succession of larvae is produced during the life of the insect."—E. E. G.

Bangalore, when as early as 1913 the degeneration had already taken place all over Mysore and Coorg. In Bangalore itself, specimens from the same locality and elsewhere show the degeneration.

The variability in the number of segments in the antennae appears to be of frequent occurrence in the genus *Lecanium*, and also in *Pulvinaria*. I tabulate below the *variations* noted by Mr. Newstead in his book on "The Coccidae of the British Isles," and by Green in his "Coccidae of Ceylon," the only literature on the subject to which I have been able to gain access.

From "The Coccidae of the British Isles."

	Normal No. of Segments.	Abnormal No. of Segments.	Remarks.
Pulvinaria vitis	8	6	
„ *floccifera*	8	6	
Lecanium persicae	7	6	
„ *ciliatum*	8	7	
„ *bituberculatum*	8	7	
„ *capreae*	7	6 or 8	
„ *nigrum*	7	8	

From "The Coccidae of Ceylon."

	Normal No. of Segments.	Abnormal No. of Segments.	Remarks.
Pulvinaria tomentosa	8	7	
Lecanium capparidis	6	7	
„ *formicarii*	8	7	
„ *acuminatum*	6	7	
„ *viride*	7	8	through incomplete division of the 4th.
„ *discrepans*	7	8	from an obscure division of the 7th.
„ *marsupiale*	7	8	
„ *bicruciatum*	6	7	
„ *longulum*	8	9	probable.
„ *psidii*	7	8	

An analysis of these variations shows that of the total number of 51 species (42 *Lecanium* and 9 *Pulvinaria*) described in the two books there is variation recorded in 17, viz. $33\frac{1}{3}$ per cent. of the number. Of these 17, the variation is by the addition of a segment in 12, by the reduction of a segment or two in 4 and by both in 1. It is thus clear that the reduction from seven to three in *Coccus viridis* cannot be placed in this category, but has

to be classed separately, not only because the reduction is by as many as four segments, but also because it is inherited. There are only two cases on record which may be held to approach this one, which I have not included in the analysis above. These are *Coccus acutissimus* and *Paralecanium* (*Lecanium*) *expansum*. In the former Green could only distinguish two basal segments, but he noticed "lighter transverse marks which suggest an original division into six or seven segments." The antennae of *Paralecanium* (*Lecanium*) *expansum* are described as "with incomplete divisions, though a terminal one and a basal two can easily be distinguished." Whether the nymphs of these two species were examined by Green is not definitely stated. But the fact that there were traces of six or seven segments in one and a terminal fourth in the other makes it probable that, at any rate at the time the species were described, the nymphs had six-segmented antennae. And it is improbable that Green would have omitted to examine the nymphs of the only two species in which there is a reduction of antennal segments beyond what he himself gives as the normal number for all nymphs of the family *Lecaniinae*.

The reduction from seven to three segments in the Mysore form must therefore be held to be unique. The fact that it is inherited by the nymphs renders no longer tenable the character of a six-segmented antenna in the nymphs as a feature of the genus *Lecanium*. The Mysore form is therefore entitled to specific rank, and I propose to name it *Coccus colemani* in honour of Dr. Coleman, as a mark of gratitude for the valuable scientific training I have received at his hands.

Coccus colemani, sp. n. (Plate V, figs. 2, 3.)

Adult ♀ characters as in *Coccus viridis*. But antennae three-segmented, the first and second segments subequal, the third from five to six times the length of the first and having a number of apical and subapical hairs. The dorsal x-wise carina not found in any stage. Dermal cells more round than oval, scattered over the derm and from 30 to 80 μ apart.

Colour pale lemon-yellow to greenish-yellow. Shape oval, the anterior end being narrower but is liable to variation in specimens fixed on the sides of veins of leaves in which the anterior end is more or less acuminate, and either the right or the left side may be

shortened and straight. The insect is ovoviviparous, but a few eggs may be found laid occasionally. Reproduction continues for about a month and a half after reaching the adult stage. The number of young produced may reach over 500.

The newly hatched larva is of a pale greenish-yellow, broadly oval. The antennae three-segmented as in the adult. The relative lengths of the segments as in the adult. Other characters as in the nymphs of *Coccus viridis*. Male unknown.

Length of adult 2–4 mm.

It may perhaps appear necessary to create a separate subgenus for the reception of this new species, but I cannot decide the question until I have made a more detailed study of the group and examined *C. acutissimus* and *P. expansum*.

The sudden formation of *C. colemani* made it appear probable that *Coccus viridis* was unstable. Green himself says that a new variety of his species was created by Mr. Newstead from specimens obtained from Lagos, but "that sufficient material was not examined to establish the fact." The report of the Department of Agriculture, Uganda, for the year 1916 states that a new form of "green bug" found along with the typical form but with eight-segmented antennae and described by Mr. Newstead originally as a subspecies has been given specific rank under the name *Coccus africanum*. There was therefore considerable justification for the belief that *Coccus viridis* was a mutating species. Requests for specimens were therefore made to the Entomologists of the Agricultural Departments of all countries where green bug occurs, but so far they have been received only from Ceylon, Java, Hawaii, Seychelles, and Honolulu. Samples sent from Uganda were unfortunately lost in transit. The material obtained is of very great interest.

The specimens from Ceylon, Hawaii, Seychelles, and Honolulu are all true to the description of Green. The Javan specimens, on the other hand, exhibit an enormous variation. Prof. Keuchenius of Java remarks in a letter received from him that "the variability of *Lecanium* (*Coccus*) *viride* is a difficult and troublesome question. Green in his standard work does not mention at all any variability, and therefore in the beginning I thought that I had to do with two different species, but afterwards I

came to the conclusion that *Lecanium* (*Coccus*) *viride* varies strongly. On the same locality and the same garden and the same kind of Coffee (but different trees) one may distinguish the following forms—

"1. A large form with a very flat body, which is of a clear green colour.

"2. A smaller form with a more elevated body, which is less acuminate in front and of a darker dirty greenish colour. Between these extremes there exist all kinds of nuances."

The following are the descriptions of the two forms referred to in Prof. Keuchenius's letter.

The Round Form. (Plate VI, fig. 1.)

The margin nearly circular. The marginal setae stout and frayed. The skeleton is thick. The dermal cells large, irregularly oval towards the margin, approximate, and smaller and more circular towards the centre. Body elevated to give a more or less elevated shape. Colour dull brown to dull yellow. The loop more or less inconspicuous. Dorsum thrown into minute transverse folds. Antennae very variable in number and relative length of segments, the more usual number eight. Measurements:—

Length/Breadth: 3/2·2, 5/2·5, 3/2·25, 2·6/1·75, 2·5/1·75, 2·5/1·75, 3·25/1·75, 3·25/2, 3/2, 3/2, 3/2, 3/2, 3/2, 3/2, 2·5/1·6, 3·25/2, 3·25/2, 3·25/2, 3·25/2, 2·6/1·75, 2·25/2, 3/1·75, 3·25/1·75, 2·25/1·75, 3/1·75, 3/2, 2·25/2, 2·5/1·5, 3/1·75, 3/2, 2/1·75, 2·6/2, 2·5/1·75, 3/2, 3/2 mm.

The Flat Oval Form. (Plate VI, fig. 2.)

Oval, flat, anterior extremity subacuminate. The marginal setae less strongly developed but of the same shape as the round form. The loop more or less conspicuous. The chitinous skeleton thinner, and the dermal cells round, fewer, scattered and not approximate. Colour varies from greenish-yellow to greenish-blue. Dorsum not thrown into folds. Antennae more usually eight-segmented, but very variable in number and relative length of segments.

Measurements:—

Length/Breadth: 4/2, 4/1·75, 4/2, 4·6/2, 3·5/2, 3·55/2, 3·25/2, 4/2, 4/2, 4/2·20, 3/1·75, 3·5/2, 4/2, 3/1·75, 2·75/1·75, 3/2, 2·75/1·75, 3/2, 2·75/2, 2·75/1·75, 3·20/2, 3·5/2, 3·25/2, 3·5/2·25, 2·75/1·75, 4/2, 3/2, 3·25/2, 3·5/2, 3/2, 3/1·75, 3/2·25/2·25, 3/2, 3·5/2, 2·75/1·7, 4/2 mm.

The antennal variability in these two forms is very great and is disclosed by the following analysis :—

Round Form (of 25 examined).				Long Form (of 33 examined).			
Antennae	8	segmented in	15	Antennae	8&8	segmented in	16
,,	8&7	,,	3	,,	8&7	,,	6
,,	8&6	,,	1	,,	7&7	,,	8
,,	7&7	,,	1	,,	7&6	,,	2
,,	6&6	,,	3	,,	5&5	,,	1
,,	6&5	,,	1				
,,	5&5	,,	1				

From this it appears that among the round form, of the 25 examined 10 had abnormal antennae, or 10 per cent. In the long form of 33, 17 had antennal abnormality, or 51·5 per cent. The range of variation as shown in the charts (Pl. VII, figs. 1 and 2) is very great and far exceeds the limits of ordinary variation. It is not alone that segments show a reduction in number and relative length, but in the same specimens the antennae may be different in the number and relative length of segments, producing an asymmetry. The variability in size, colour, shape and elevation appears to continue to the same extent in the specimens sent by Prof. Keuchenius in 1916 as when he studied the pest two years previously.

Between these two varieties described above, there are several intermediate forms, presenting several stages and gradation in details of structure, size, colour, elevation and conspicuousness of the loop, but they are mainly grouped round these two types. From a study of the material the impression is forced on one that the Javan forms are highly unstable. Two of these forms described above are entitled to specific rank. One of these, the oval flat form, may prove identical with the new form described by Mr. Newstead as *Coccus africanum*. The other has, so far as I am aware, not been described. I refrain from creating species for the reception of these two, until I have an opportunity to examine *Coccus africanum*.

These facts of variation prove that *Coccus viridis* is a mutating species. In Mysore the bug was all but caught in the act, and in Java the saltatory variations continue. In Uganda a new form has been in existence since 1898, when *C. africanum* was first described as a subspecies.

There are two views possible in regard to this interesting

phenomenon: (1) that *Coccus viridis* produces different forms under the stimulus of different conditions; (2) that *Coccus viridis* itself is a mutant from another unstable species. One or both these may be true. If *Coccus viridis* and the forms regarded as its derivatives all maintain the distance from other species, which entitled it to specific rank, then the inference is justified that the mutating species is *C. viridis*. If, on the other hand, *C. viridis* or one of its so-called derivatives structurally approaches or is very nearly identical with another species of scale insect and this latter is an unstable species, then it follows that the mutating species need not be necessarily *C. viridis* alone, but the species with which *C. viridis* or one of its derivatives is found to closely agree.

We have now to see which of these alternatives has application in regard to the variations described above. The flat form from Java, the South Indian form, the *Coccus africanum* of Uganda, are more or less referable to *Coccus viridis*. But the round form from Java is different in structural detail. The round contour is not a great difference, for it has been found occasionally among the South Indian forms. The eight-segmented antennae are common to *C. africanum* and to the oval flat form from Java itself. The antennae are just like those of *P. psidii*, as will appear from the charts (Pl. VII). The irregularly oval approximate dermal cells and the strongly developed marginal setae are peculiar to the round form, which makes it structurally identical with *P. psidii* as it occurs in Mysore. Specimens of these placed under the microscope so approach each other in structure that it would be difficult to tell the difference except from the contour, which is round in one and oval in the other. It is not known what shape *P. psidii* takes in Java, but the shape is as already indicated of very little consequence.

The structural similarity of the round form with *P. psidii* assumes a new significance and importance when the variability of *Pulvinaria psidii* is considered. Its variability is a feature of this bug which Green himself has noticed both in regard to size and anal plates. After noting a minor variation in the length of the fourth segment, he proceeds: "Valves of the anal operculum variable in form in the same community and is particularly marked in some examples from myrtle, of which no two individuals are identical in this particular. . . . Length of insect

averaging from 3–3·50 mm., but exceptionally large individuals have reached 5 mm., some examples from myrtle, while showing all the structural characters of the type, were exceptionally small, the adult insect only measuring 2 mm. in length, with a correspondingly small ovisac."

To these variations have now to be added those of the antennae, which as shown in the drawings are reduced from the normal eight to as low as five (Pl. VII, fig. 4). In the same specimen, as in the Javan form, one antenna may vary in one direction the other in another. Here, again, the reduction may be greater than that which has ever been noticed in other species of *Pulvinaria*, for in *psidii* it may be by as many as three segments, whereas in other species of the genus it is never greater than by one or two segments.

These variations reduce the gap between *P. psidii* and *C. viridis*. The differences between the two species are tabulated below.

P. psidii.	*C. viridis.*
Shape oval, not variable.	Shape variable, one side straight the other curved, rarely oval.
Colour varies from dark or dirty green to greenish-yellow, very variable. Dull.	Greenish to pale lemon-yellow. Not very variable. Shiny.
Antennae 8-segmented.	Antennae 7-segmented.
Oviparous.	Ovoviviparous.
Secretes meal to lay eggs in.	Does not secrete meal.
Chitin thick, loop therefore invisible.	Chitin thin, loop therefore visible.
Dermal cells large, irregularly oval, approximate towards the margin, but more or less round towards the centre.	Dermal cells round.

The distinction between the antennae is of little importance in view of the variation in both the species. It has already been shown that antennal segments in *Pulvinaria psidii* may be reduced to as low as five. As regards mode of reproduction, though no *P. psidii* has shown any departure from oviparv it is not unusual to find beneath green bugs a few developed eggs. The majority of species in the genus *Lecanium* are oviparous. Therefore it appears

to me that the ovovivipary of *viridis* is an advanced stage transitional from oviparv. With regard to the loop the presence or absence of it is by itself an unimportant distinction as it is only the appearance of the Malpighian tubes which will be visible or invisible according as the chitin is thin and transparent or thick and opaque. The variations in *P. psidii* are so great that those of *C. viridis* come within their limits. A similar remark holds good in regard to size. The difference in the shape of the dermal cells is not great. There are specimens of *C. viridis* in which the dermal cells distinctly approach the shape and arrangement in *P. psidii* (Pl. V, fig. 1). The main distinction on which Green appears to rely is, that *P. psidii* secretes meal and *viridis* does not. But this distinction breaks down, for in *L. hemisphaericum*, as I have found, and as Green himself has observed, there is a secretion of meal along the margin. Green says in regard to it that "at this time (of gestation) the inner marginal surface is dusted with white mealy powder, and where a scale has been detached from the plant, an oval white ring marks the previous position." As a matter of fact the secretion of meal is in much greater quantity than indicated in this description, in specimens of *L. hemisphaericum* from Mysore (Pl. VIII, fig. 1).

There is also the fact that one apparently healthy mealy bug has been discovered by me to lay eggs beneath the body without a preliminary secretion of meal. Diseased specimens have also been occasionally observed to lay eggs without secreting meal. Furthermore, in green bug there appears to be a secretion of meal, though in the minutest quantity. When specimens are lifted off from the leaf they do not always drop to the ground but often hang by a thread, which must therefore be secreted by the bug itself,* and Green notices the presence of wax-secreting glands round the reproductive opening. The resemblance goes further. I have already remarked on the feature of *psidii* of being tilted at an angle to the surface of the host by the secretion of meal beneath. This habit has been found in large numbers of green bug.† In other species

* I think that the author has misinterpreted this phenomenon. When one of the insects is detached without unnecessary violence, it will often remain hanging by its long rostral filaments, which are inserted into the tissues of the plant.— E. E. G.

† The "tilting" of the body, in *L. viride*, is usually a symptom

of *Lecanium* (*Coccus*) in Mysore this habit has not been found or is slight and inconspicuous. In *Coccus viridis* it is so great that the dorsum may be thrown into minute folds (Pl. VIII, fig. 3). It is difficult to explain this except as an inherited tendency persisting after the necessity has disappeared.

If the difference between *psidii* and *viridis* appears, then, of little importance, the difference between *psidii* and the Javan round form is much less. The structural characters of these two are, as I have already shown, identical. The only serious difference is in the method of reproduction. The Javan round form is thus intermediate between *psidii* and *viridis*. The series of forms commencing from *psidii* on one side and extending to *viridis* and *colemani* on the other, exhibit a gradual degeneration not by fluctuating variation but by saltatory variations, or what De Vries would call retrogressive mutations. For, on the one side, we have a meal-secreting habit, more numerous and larger cells in the derm, strong marginal setae, a larger size, and eight-segmented antennae, and at the other end a smaller size and three-segmented antennae, absence of meal, less numerous and more rounded cells in the derm and very feebly developed marginal setae. The intermediate types approach one or other of these extremes, and some of them are extremely unstable. The conclusion appears therefore to be justified, that *Coccus viridis* arose as a mutant from *Pulvinaria psidii*, and the various forms from South India, Java and Uganda are derivatives from the latter species either directly or through *C. viridis*.

This hypothesis that two species which are placed in different genera have mutational relations is the only one that fits the facts given above. Short of actual demonstration, it is difficult of acceptance at first sight, and demonstration is difficult under the widely different conditions of distant countries in which the mutations have occurred. It does not appear probable that the various forms so produced can all be produced in one of these, especially when the parthenogenetic condition of these forms prevents their crossing. South India yields only

of disease, and commonly occurs in the incipient stages of infection by the parasitic fungus *Cephalosporium*. I have never observed a healthy insect in this position.—E. E. G.

one form; so also Ceylon. In Uganda the two types are probably fairly fixed. Java, where the types are not yet fixed and where the closest approach to *psidii* is found, seems to be the most promising field for the experimental demonstration of a common origin of the various forms, though it appears unlikely that *Coccus colemani* will be produced there.

Until these experiments are conducted in Java or elsewhere (some of these are being attempted in Mysore), I must look for confirmation of my hypothesis in facts which have already been recorded by Coccidologists.

With regard to the two genera *Pulvinaria* and *Lecanium*, Green writes as follows in his book on "The Coccidae of Ceylon," p. 258: "In all purely structural characters there is nothing to distinguish the members of this genus (*Pulvinaria*) from those of *Lecanium*, so much so that until the period of oviposition it would be impossible to determine whether an individual should be placed in one genus or the other," and later, on p. 264, when dealing with *P. psidii*, he says, that "in its earlier stages the insect bears a superficial resemblance to *Lecanium* (*Coccus*) *viride*, from which it may be distinguished by the absence of the dark intestinal loop."

Newstead is even more emphatic. He says in his book on "The Coccidae of the British Isles," that "this genus comes very near to *Lecanium* (*Coccus*), and is only separable from it by the formation of a cottony ovisac below and behind the posterior extremity of the body of the adult female at the period of parturition. . . . All the stages of the male, including the glassy puparium as well as those of the female *up to the time of parturition*, are inseparable from those of *Lecanium* (*Coccus*), so that in the absence of the ovisac it is quite impossible to fix this otherwise conspicuous genus." The secretion of meal is found in another important genus, *Protopulvinaria*, in which the meal is smaller in quantity, but is secreted all round the margin. This genus has indeed been placed by Mrs. Fernald under *Pulvinaria* as a subgenus, and I have already referred to the secretion of meal in a species belonging to *Lecanium*, viz. *L. hemisphaericum*. The secretion of meal is not, therefore, an exclusive feature of *Pulvinaria*, but is found more or less in the allied genera and in *Lecanium* (*Coccus*) itself.

To turn now to the genus *Pulvinaria*, the variations I

have indicated are in individuals. In a mutating species, especially when it is found all over the world, there must be well-marked varieties, and this is what we find. Apart from the "phytophagous" varieties, which are very numerous in Mysore, there are others of a more permanent character. The form of *Pulvinaria psidii* in the Philippines has been given subspecific rank by Cockerell under the name *philippina*. He says in his monograph on "Coccidae from the Philippine Islands" (Putman Memorial Fund, 1905), "the long tibia, long third antennal joint, marginal hairs, long bristles on joints 2 and 5 of antennae, etc., all show this insect to be very close to *Pulvinaria ficus* (Hempel) and *P. psidii* (Maskell). The six-jointed antennae are distinctive, but may not be constant. It is evidently reasonable to treat this insect as a subspecies of *psidii*, and so far as I can make out *P. ficus* should stand as *P. psidii ficus*." That is to say, there are two well-marked subspecies in *P. psidii*. With regard to a third species, *P. cupanae*, Green says that it is doubtfully distinct from *P. psidii*.

A more striking evidence of the consanguinity of the various types I have dealt with is the variability of the anal plates in all of them. Green says in his introduction to the family *Lecaniinae* that their form and size afford good specific characters. These characters do not vary with the size of the individual, but are practically constant for each of the several stages, and on p. 236, in describing the variety "*quadratum*" of *Lecanium expansum*, he says, "the size and form of the anal scales of the adult female are usually so constant in any one species of *Lecanium* that such a marked difference as is found in the present instance must be looked upon as varietal." Green has recorded the variability of the anal plates in *P. psidii* and given drawings of the various shapes they assume. The quotations above indicate that this variability is an indication of great instability. Now in the types which I regard as derivatives of *P. psidii* it is not alone that the anal plates are of the same shape when normal, but the variations when they occur are more or less in the same direction. They are more fixed in the more stable forms as *Coccus viridis*, less fixed in *Coccus colemani*, and least in the forms from Java. The shape of the anal plates and their variability in the same direction is quite consistent with the hypothesis I have advanced of a common origin.

The tendency to regressive mutation exhibited by these insects is probably due to the continued absence of a sexual generation, which, if one may judge from the behaviour of species similarly circumstanced, tells on the vigour and vitality of the species. Though *C. hesperidum* is one of the commonest species occurring on numerous plants from the United States to Japan, no male has been recorded at any rate from India, Java or Ceylon; nor have males been recorded for *C. viridis*, the study of which dates as far back as 1882, except for two doubtful ones from Java.

The Weismanian theory that the purpose of sexual reproduction is to induce variability has received no support from the study of variation in parthenogenetic forms, the results of which show that variability in such species is not less than that in sexually produced forms, and that therefore variability is not a factor necessarily introduced by the union of the sexes. But from the fact that parthenogenesis does not induce variability it does not follow that it is the cause of it. I suggest it as a possibility because the types I have been dealing with show a progressive degeneration, and because it seems to me that the continued absence of a male generation prevents the swamping effects of intercrossing, and therefore affords a greater chance for the survival of variations. Whether or not the continued absence of a sexual generation is the real explanation of the instability of *P. psidii*, it is the sort of species where one would look for mutation. Much the same remarks apply to *C. viridis*, which take so many different forms in different countries. There is thus considerable justification apart from the facts I have already given for the conclusion that *C. viridis*, *C. colemani*, *C. africanum*, and the Javan forms are directly or indirectly derived from *P. psidii*.

This conclusion is of great importance and interest. It indicates that the parallelism in structure between genera with ovisacs and those without them have an evolutionary connection, the ovisac condition being antecedent in time. Such genera could be found in families other than *Lecaniinae*. In *Dactylopinae*, for instance, there is a structural similarity between one oviparous and another viviparous species in Mysore. In *Pulvinaria* itself, there are probably other species which stand to species in *Lecanium* in the same relation as *psidii* does to *viridis*. In

Mysore there is at least one instance where such relation appears to occur. This is under investigation. It is significant in this connection that there are several species in *Pulvinaria* in which there are well-marked varieties. Newstead merges in *Pulvinaria vitis* the following species, *P. betulae*, *P. salicis*, *P. oxyacanthae*, and *P. persicae*, but retains *P. ribesiae* as a variety. Similarly the limits of variation are great in *P. floccifera*, in which also a number of species have been merged. The study of species like these will throw considerable light on the relationships of the various genera and species of *Coccidae*.

Even more important and valuable will be the instances of mutation which the study is likely to bring to light. I give below two instances which furnish a very close parallel to the phenomena which I have described, where therefore mutation must have occurred. In a most interesting paper on "Some comparisons of *Coccus citricola* and *C. hesperidum*," Mr. H. J. Quayle, of the University of California, gives an account of the relationships between the two species, which are almost similar to those between *P. psidii* and *C. viridis*. I summarise below the differences between the two species.

C. citricola.	*C. hesperidum.*
Antennae with 8 segments in the great majority.	Antennae with 7 segments.
Ground-colour grey or dirty white. A more even distribution of dark colour pigment.	Ground-colour distinctly yellowish. Colour pigment coalesced in more or less definite areas.
Lustre dull.	Lustre shiny.
Shape oval, not variable.	Shape variable: one side straight, the other curved.
Male found occasionally.	Male unknown.

C. citricola is the more variable of the species. Quayle says: "In 78 specimens of *citricola* in which 139 antennae were examined there were three scales each with seven joints in one antenna and eight in the other. In four scales there were seven joints in both antennae, and in four others there were seven joints in one antenna, while the other was not examined. The remaining number, or 67, had eight joints in both antennae. In 73 specimens of *hesperidum* examined all had seven joints." The paral-

lelism between *C. citricola* and *C. hesperidum*, on the one hand, and *P. psidii* and *C. viridis*, and *C. viridis* and *C. colemani*, on the other, will now be obvious. There is one apparent difficulty. *Citricola* is a species described in 1914, but *hesperidum* was described many years earlier. According to my hypothesis *citricola* should be regarded as the parent species and as having been earlier in time. It has, however, to be remembered that the mere fact of an earlier record is of itself insufficient to prove the later origin of a species. What has probably happened is that *hesperidum* formed out of *citricola* crowded out the parent species, and this would fit in exactly with my hypothesis and with the observations in Mysore and other countries where *Pulvinaria psidii* is seldom a pest, while *C. viridis* and *C. colemani* are notoriously injurious to crops.

The second instance is that which has come to the notice of Green, and to which he refers in the course of an interesting letter received from him on the subject of the phenomenon in *C. viridis*, brought to his notice. He wrote as follows: "Such degeneration, if clearly established, is extremely interesting, and so far as I know has not been recorded before. Curiously enough since reading this paper I have met with an instance that appears to be of a similar nature. In examining some old material from Java, I have found an insect that agrees in every character with *Phenacoccus mangiferae*, described from Ceylon, except that its antennae have only seven instead of nine joints. According to the present classification, this difference would necessitate the relegation of the Javan specimens to a distinct genus (*Pseudococcus*). But I am convinced that they are really conspecific."

What has undoubtedly occurred in *C. viridis* is therefore by no means an isolated instance, and I believe the study of scale insects in the light of the phenomenon recorded and described above will bring to light more instances of mutation. We are still too ignorant of the obscure processes involved in this important phenomenon to neglect what seems to me to be a promising field for its investigation.

In conclusion, I have to thank Dr. Coleman, the Director of Agriculture in Mysore, for his sympathy and guidance, and through him Prof. Kenchenius of Java, Mr. C. C. Gowdey of Uganda, Mr. Lyne, Director of Agriculture in Ceylon, Mr. P. R. Dupont, Curator, Botanic Station,

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Explanation of Plates V–VIII.

Plate V, fig. 1. *Coccus viridis*, one of the first specimens sent in for identification on the outbreak of the pest in Mysore in 1912. Fig. 2. *Coccus colemani*. Fig. 3. *C. colemani*. Fig. 4. Larva of *C. colemani*, just hatched. Note that there are only three segments in the antennae.

Plate VI, fig. 1. The round form from Java. Note the dermal cells. Fig. 2. The long form from Java. Note dermal cells. Fig. 3. *P. psidii*. Fig. 4. *Pulvinaria psidii*.

Plate VII, fig. 1. Antennae of the long form from Java. Fig. 2. Antennae of the round form from Java. Fig. 3. Antennal variation in *P. psidii*, round form from Java, *C. viridis*, *C. colemani*. Fig. 4. Variation in the antennae of *P. psidii* and stages of reduction from the antennae of *C. viridis* to the antennae of *C. colemani*. Fig. 5. Antennal variation in the abnormal round form from Java, and the abnormal long form from Java.

Plate VIII, fig. 1. *L. hemisphaericum* turned over to show the waxy secretion along the margin of the body, and the mark left on the leaf as a result of the filaments adhering. Fig. 2. The secretion of meal in *P. psidii*. Fig. 3. *C. viridis* showing the hind end of the body tilted up much as in *P. psidii*. Fig. 4. Variations in the anal plates of *P. psidii* from Green, of *P. psidii* from Bangalore, *C. viridis* from Ceylon, and *C. viridis* from Bangalore.